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The Taxonomic Value and Variability of Certain Structures in the Cestode Genus *Echinococcus* (Rudolphi, 1801) and a Review of Recognized Species

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THE TAXONOMIC VALUE AND VARIABILITY OF CERTAIN STRUCTURES IN THE CESTODE GENUS *ECHINOCOCCUS* (RUD., 1801) AND A REVIEW OF RECOGNIZED SPECIES

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Although cestodes of the genus *Echinococcus* have been much studied in the past, there is need for an evaluation of these morphological characters used as the basis for species differentiation. The generous co-operation of other investigators in providing necessary foreign material and the results of nearly five years of field work in Alaska make possible such a study. It is the purpose of the paper to evaluate morphological characters used at the species level to differentiate these cestodes, and to review the status of species currently considered valid.

This paper is written in appreciation of the significant contribution to helminthology made by Professor Gobind Singh Thapar.

MATERIAL AND METHODS

Seven species of *Echinococcus* are considered valid: *E. granulosus* (Batsch, 1786); *E. oligarthrus* (Diesing, 1863); *E. longimanubrius* Cameron, 1926; *E. minimus* Cameron, 1926; *E. cameroni* Ortlepp, 1934; *E. lycaontis* Ortlepp, 1934; *E. felidis* Ortlepp, 1937. Of these, preserved material, unmounted, has been available for all species except *E. longimanubrius* and *E. minimus*. In addition, material representing a distinct, but yet unnamed, species from St. Lawrence Island, Alaska, has been studied.

The cestodes were stained with Semichon's acetic carmine and Ehrlich's acid hematoxylin, cleared in terpineol, and permanently

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mounted. Accurate observations on rostellar hooks were made by mounting detached scolices separately. Adequate pressure was applied to such preparations to cause the rostellar hooks to lie flat on the slide.

In addition to material made available by other investigators, specimens obtained at autopsy of domestic and wild canine animals in Alaska have been utilized. More important for the purposes of this work has been material obtained through the experimental infection of dogs and foxes. Such cestodes were removed from the intestine immediately after the death of the host animal. These cestodes were allowed to relax in cold water, and were fixed by sudden immersion in hot formalin-acetic acid-alcohol solution. Since these experimental infections were of known duration, actual age of the cestodes could be considered.

Two species were used in the experimental work: (1) *E. granulosus*, which occurs naturally in boreal North America, and parasitizes in the intermediate stage wild ruminants (*Alces* and *Rangifer*); (2) *Echinococcus* sp. indet., which occurs on St. Lawrence and the Komandorskii Islands, in Bering Sea, intermediate hosts being voles (*Microtus* and *Clethrionomys*).

Experimentally-obtained cestodes of these two species have been used for most of the observations on morphological variation. Additional data have been obtained from specimens of *E. granulosus* and *Echinococcus* sp. from various naturally-infected carnivores in Alaska. Specimens of *E. granulosus* from other parts of the world have also been studied.

Results

The characters which have been used to differentiate the species of *Echinococcus* are discussed separately.

Morphological Characters

Length of strobila. Specimens of *E. granulosus* ranging in length from 1 to 6 mm. have been obtained from natural infections of Alaskan carnivores. In general, the larger individuals occur in the relatively large

host species (e. g., wolf and dog), and the smaller worms occur in foxes (both *Vulpes* and *Alopex*). Considerable variation is noted in relative massiveness of strobilae from different animals.

In the specimens obtained from dogs experimentally infected by *E. granulosus*, strobila length ranged from 4 to 6 mm. Adult size is attained within 40 days, under experimental conditions. No senile worms were studied, since all dogs were destroyed at a relatively early time after infection. Species of the same form from jackal (*Canis*) and domestic dog from South Africa, and from domestic dogs from Argentina, showed the same size range—4 to 6 mm.

Observations were made also on the St. Lawrence Island form of *Echinococcus*. In natural infections, from both dogs and foxes (*Alopex*), the cestodes ranged in length from 1.2 to 2 mm. Size differences related to occurrences in these two host-species were not apparent. In experimental infections in *Alopex*, the cestodes attain an average size of about 2 mm. in five weeks. Strobila length is to a degree correlated with age of the individual cestode. The worms become senile as early as three and one-half months after infection of the final host. These senile cestodes show greatly reduced egg production, increase in segment number, and relative increase in length of segment. A total length of nearly 4 mm. may be attained by these older worms. Development of the uterus takes place in as many as three segments, but no eggs, or very few, are present. In segments which appear mature, the reproductive organs are not well developed, and give the impression that normal activity is no longer taking place. Such cestodes are gradually eliminated after reproduction stops. Observations made as long as seven months after the establishment of infection disclosed that all worms may have been eliminated; in some animals, a few worms containing no eggs may persist.

Segment number. Segment number appear to be relatively uniform for a given species if only those specimens showing maximum reproductive activity are considered. Two or three segments are found in both *E. granulosus* and *Echinococcus* sp. (St. Lawrence Island). It is concluded that segment number, in combination with other characters, probably has value in the differentiation of the species of *Echinococcus*, if only sexually active individuals are considered,

Size of rostellar hooks. Hook size has been considered especially important in the taxonomy of cestodes of this genus. However, it is apparent that hook length is subject to rather extreme variation.

Age of the individual cestode must be considered as affecting hook size. It is generally accepted that the blade of the hook attains full size in the larval stage of *E. granulosus*, but that subsequent growth in the handle and guard occurs after ingestion of the larval cestode. The writer's observations seem to support this view insofar as *E. granulosus* is concerned. Infective larvae taken from the lungs of *Alces alces* possessed hooks with average measurements as follows: large hooks, 30 μ; small hooks, 25 μ. Adult cestodes obtained through feeding larvae from the same host animal showed the following average measurements: large hooks, 37.6 μ; small hooks, 30 μ.

With the St. Lawrence Island material, however, this difference does not exist. Hooks of the larvae used experimentally to infect foxes (*Alopex*) had the following average measurements: large hooks, 26.9 μ; small hooks, 22.6 μ. Hooks of the adult cestodes averaged nearly the same: large hooks, 27.3 μ; small hooks, 21.6 μ.

It should also be pointed out that apparently anomalous hooks may often be observed. These may be unusually small, but with normal proportions, or they may be much distorted,

It is concluded that hook size, if established on worms having matured eggs in the uterus, has some value as a specific character. However, it has been found in connection with other species of cestodes that "populations" of relatively local distribution are morphologically uniform, but may differ considerably from other "populations" over a wide geographical area (see Rausch and Schiller, 1949; Rausch, 1952 a; Schiller, 1952). Hook size in *E. granulosus* seems to follow this pattern of geographical variation, so it is necessary to take this into consideration when attempting to identify cestodes of this genus. This is particularly important in the absence of other characters of value. In *E. granulosus* from various hosts and geographic localities, large hooks have been found to range from 26 to 42 μ, and small hooks from 22 to 35 μ.

Hook shape. The shape of rostellar hooks is variable in cestodes of the genus *Echinococcus.* This situation is not uncommon, and occurs as well in the members of the closely related genus *Taenia.* Some concept of variation of hook shape in *E. granulosus* may be had from Plate I, Figs. 1-5. Minor differences in hook shape are not significant; however, each species of *Echinococcus* recognized below possesses rostellar hooks of characteristic pattern.

Testes number. The number of testes in mature segments of *E. granulosus* is relatively uniform. In cestodes from both dogs and wolves from mainland Alaska, the testes number ranged from 45 to 65; the average number is about 56.

Testes number was observed also to be relatively uniform in cestodes from St. Lawrence Island. Specimens from both dogs and foxes (*Alopex*) showed numbers ranging from 17 to 25, with an average of about 22.

Foxes (*Vulpes*) from mainland Alaska and Nunivak Island (Bering Sea) have been found to harbor very small cestodes which have been tentatively considered *E. granulosus.* There is no evidence to the contrary, except that these cestodes also possess relatively few testes. The possibility cannot be entirely eliminated at this time that this form is identical with that occurring on St. Lawrence Island. It is of interest that cestodes from a fox from Switzerland closely resemble the Alaskan specimens in testes number. Since *Echinococcus* larvae of the alveolar type have been rather frequently reported from man in Switzerland, and since Dr. J. G. Baer (personal communication) has recently obtained a vole infected with the larval stage of *Echinococcus* sp., it cannot be concluded with certainty that the Swiss specimens are *E. granulosus.* Additional work, involving experimental infections, will be necessary to determine the status of such small specimens from Alaskan mainland foxes. The rostellar hooks of these specimens from foxes are shown in Plate I, Figs. 6-8.

Number of rostellar hooks. In the writer's opinion, the number of rostellar hooks is so variable as to be worthless as a specific character in the genus *Echinococcus.*

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Testes distribution. In *E. granulosus,* the testes are about as numerous anterior to the genital pore as posterior to it. In this respect it contrasts with *Echinococcus* sp. from St. Lawrence Island, in which the testes are restricted almost entirely to the posterior half of the segment. Testes distribution and other morphological details are shown for *E. granulosus* in Text Fig. 1, and for *Echinococcus* sp. of St. Lawrence Island, in Text Fig. 2.

Egg size. It was recently emphasized (Rausch, 1952a) that egg size may be highly variable, according to geographic locality, in a given species of cestode. This holds true also for *E. granulosus.* Egg size has little or no value in differentiating the species of *Echinococcus.*

Form of gravid uterus. As in the genus *Taenia,* the number of lateral sacculations on the gravid uterus of *Echinococcus* spp. has been accorded value as a specific character by some workers. On the basis of material at hand, it is concluded that form of gravid uterus cannot be relied upon as a specific character in this genus. As an example, in *E. granulosus* the gravid uterus may show a simple, sac-like form, or lateral branches may be well developed. If present, the sacculations are variable in number.

Sacculations have not been observed in the gravid uterus of the St. Lawrence Island cestodes. In pre-gravid segments, where form of the early uterus is more easily defined, sacculations are not developed.

Other organs. No significant observations have been made in connection with any other organs, either male or female. Cirrus sac dimensions may have value in combination with other characters.

The significance of Host-species occurrence

In the writer's opinion, a high degree of host-species specificity is demonstrated by members of the genus *Echinococcus.*

E. granulosus may infect several species of canine animals, but is apparently not capable of normal existence in feline species, nor in any other carnivores. Lörincz (1933) demonstrated the unsuitability of the domestic cat as host of this species. On the other hand, both *E. oligarthrus* and *E. felidis* parasitize feline animals and do not, as far

as is known, occur in canine hosts. However, the knowledge of these relationships is far from complete.

Except for *E. granulosus*, little is known regarding the mammals parasitized by the larval stage of *Echinococcus* spp. A large South American rodent (*Myocastor*) has been reported several times as harboring the larval stage of *Echinococcus* sp. The species in question appears to be *E. oligarthrus*. The larval stage of *E. felidis* no doubt occurs in one or more species of African artiodactyl or perissodactyl. This is also the case with *E. lycaontis*, which is found in Africa. *Echinococcus* sp. of St. Lawrence and the Komandorskii Islands is distinguished by the fact that its larva occurs in small rodents (*Microtus* and *Clethrionomys*). This form is further distinguished by the characteristic alveolar structure of the larva.

Further work, based on experimental infections, is needed to clarify important relationships involving the species of *Echinococcus* and their intermediate and final hosts.

The Species of Echinococcus

Among the seven species of *Echinococcus* considered here, *E. longimanubrius* Cameron, 1926, and *E. minimus* Cameron, 1926, are regarded as *species inquirendae*. Information on these forms is incomplete, and it is probable that they will be found to be conspecific with *E. granulosus*. Both species were described essentially on the basis of differences in form and size of rostellar hooks. Cameron (1926; p. 21) stated, "It seems reasonable to assume that the hooks in such a closely related genus as this is, will also within small limits remain constant in shape and size for each species." These characters have been discussed above, and it was concluded that both shape and size are variable.

On the basis of available material, and the discussions of Cameron (1926) and Ortlepp (1934), it is concluded here that the species *E. cameroni* Ortlepp, 1934, is conspecific with *E. granulosus*. Cameron (1926) discussed this material, obtained from a fox (*Vulpes*) in England, as *E. granulosus*. Ortlepp (1934), on the basis of ".....size of the parasite, the number of segments, the size and shape of the hooks....." concluded that this material represented a distinct species, and designated it as *E. cameroni*.

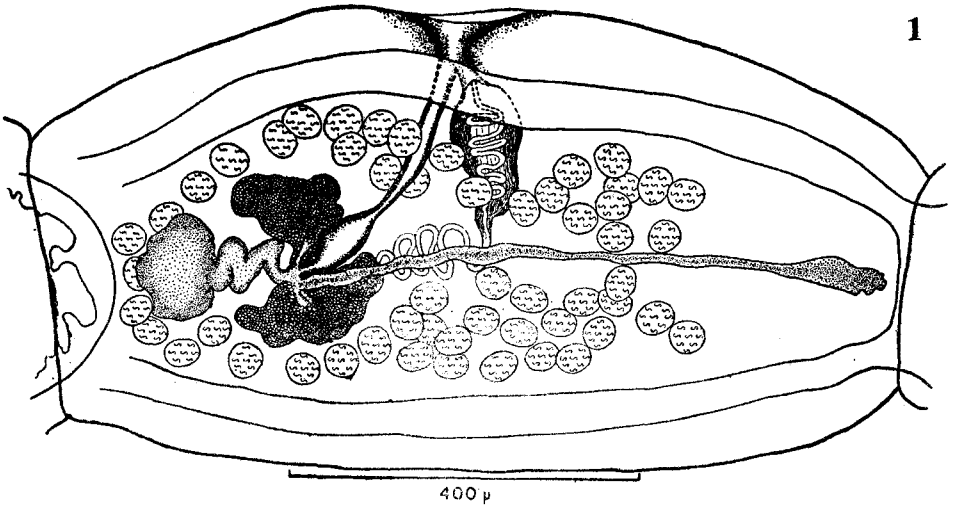
The writer's observations on the original material agree closely with those of Ortlepp. The specimens are larger than those usually seen in foxes, and the eggs average rather large (about 41×38 μ). However, testes distribution is typical of *E. granulosus*, and the characters used by Ortlepp are highly variable ones. On the basis of a more accurate valuation of these characters, *E. cameroni* cannot be distinguished and is consequently considered a synonym of *E. granulosus*.

The four species considered valid by the writer are defined briefly:

E. GRANULOSUS (BATSCH, 1786)

(Plate I, Figs. 1-5 & Text-fig. 1)

Strobila length from 1.5 to 6 mm.; segments usually 2 in number, but 3 or more may occur. Testes number ranges from 45 to 65 (av., about 56). Testes about equally distributed anterior and posterior to



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genital pore level. Cirrus sac averages about 100×70 μ. Rostellar hooks, 32 to 40 in number, somewhat variable in shape. Large hooks measure 27 to 40 μ; small hooks measure from 21 to 35 μ. Hook length variable according to geographic locality. Eggs variable in

size ; from 32 to 40 μ by 28 to 38 μ. Gravid uterus sac-like or showing lateral sacculations.

Distribution : Cosmopolitan.

Final host : Canine animals.

Intermediate host : Artiodactyls and perissodactyls.

E. OLIGARTHRUS (DIESING, 1863)

(Plate I, Fig. 9)

Strobila length from 1.9 to 2.3 mm. ; segments usually 2 in number, but 3 may be present. Testes number ranges from 23 to 29. Testes extend well anterior to genital pore, encircling female genital organs. Cirrus sac averages about 75×40 μ. Rostellar hooks 36 to 40 in number ; large hooks measure 46 to 50 μ (av., 49 μ) ; small hooks measure 36 to 39 μ (av., 38 μ). Degree of variability of rostellar hooks unknown. Eggs measure 34 to 37 μ (av., 35 μ) by 29 to 32 μ (av., 31.5 μ). Gravid uterus sac-like.

Distribution : Central and South America.

Final host : Feline animals (*Felis concolor* and *F. yaguarondi*).

Intermediate host : *Myocastor*.

E. LYCAONTIS ORTLEPP, 1934

(Plate I, Fig. 10)

Strobila length 4 to 6 mm. ; usually 5 segments present, but more may exist. Testes, about 40 in number, extend well anterior to genital pore. Cirrus sac averages about 100×60 μ. Rostellar hooks, 34 to 35 in first two rows ; of characteristic shape. Large hooks measure 36 to 42 μ ; small hooks measure 28 to 30 μ. Eggs measure 36 to 44 μ (av., 40 μ) by 32 to 37 μ (av., 34 μ). Gravid uterus shows numerous, well-defined sacculations.

Distribution : South Africa.

Final host : *Lycaon pictus*.

Intermediate host: Unknown.

E. lycaontis in some details resembles *E. granulosus,* but must be considered distinct on the basis of present knowledge. Ortlepp (1934) described this species as having accessory hooks, and the writer has also observed these. Their significance is not understood at this time.

E. FELIDIS ORTLEPP, 1937

(Plate I, Fig. 11)

Strobila length about 6 mm.; 3 to 4 segments present. Testes number from 28 to 46, about equally distributed anterior and posterior to level of genital pore. Cirrus sac averages about 150 by 100 μ; of usual shape. Rostellar hooks number from 32 to 46; hooks of characteristic shape. Large hooks measure 39 to 44 μ (av., 41 μ); small hooks measure 32 to 35 μ (av., 33 μ). Eggs measure 37 to 40.5 μ (av., 39.6 μ) by 32 to 35.5 μ (av., 33 μ). Gravid uterus shows poorly-defined sacculations.

Distribution: South Africa.

Final host: *Felis leo.*

Intermediate host: Unknown.

E. felidis is well characterized by hook shape and host occurrence.

ECHINOCOCCUS SP. INDET.

(Plate I, Fig. 12 & Text-fig. 2)

Strobila length 1.2 to 3.7 mm.; 2 segments normally present, but 3 or 4 may sometimes occur in old specimens. Testes number 17 to 26 (av., 22); distributed in posterior half of segment. Cirrus sac averages 90 by 50 μ. Rostellar hooks, 26 to 36 in number (av., 30). Large hooks measure 23 to 29 μ (av., 27) μ; small hooks measure 19 to 26 μ (av., 21.6 μ). Eggs measure 30 to 38 μ (av., 34 μ) by 29 to 34 μ (av., 30 μ). Sacculations not evident on gravid uterus.

Distribution: St. Lawrence Island and Komandorskii Islands.

Final host : Domestic dog and arctic fox (*Alopex lagopus.*)

Intermediate host : Microtine rodents (*Microtus* and *Clethrionomys*) ; several other species of rodents experimentally infected.

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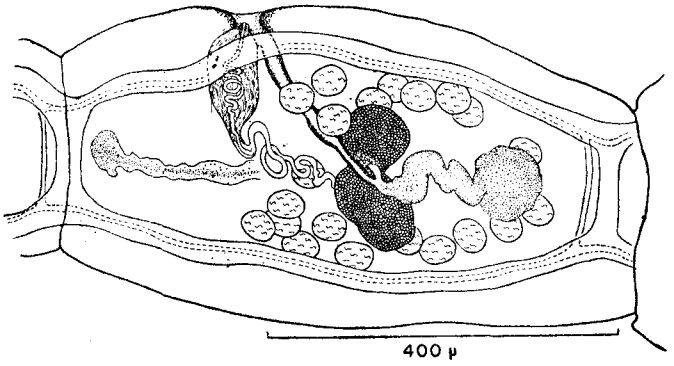

This species is undoubtedly distinct, and is probably identical with the form causing alveolar hydatid disease in man in Europe and Russia. Further discussion of this form has been given elsewhere.

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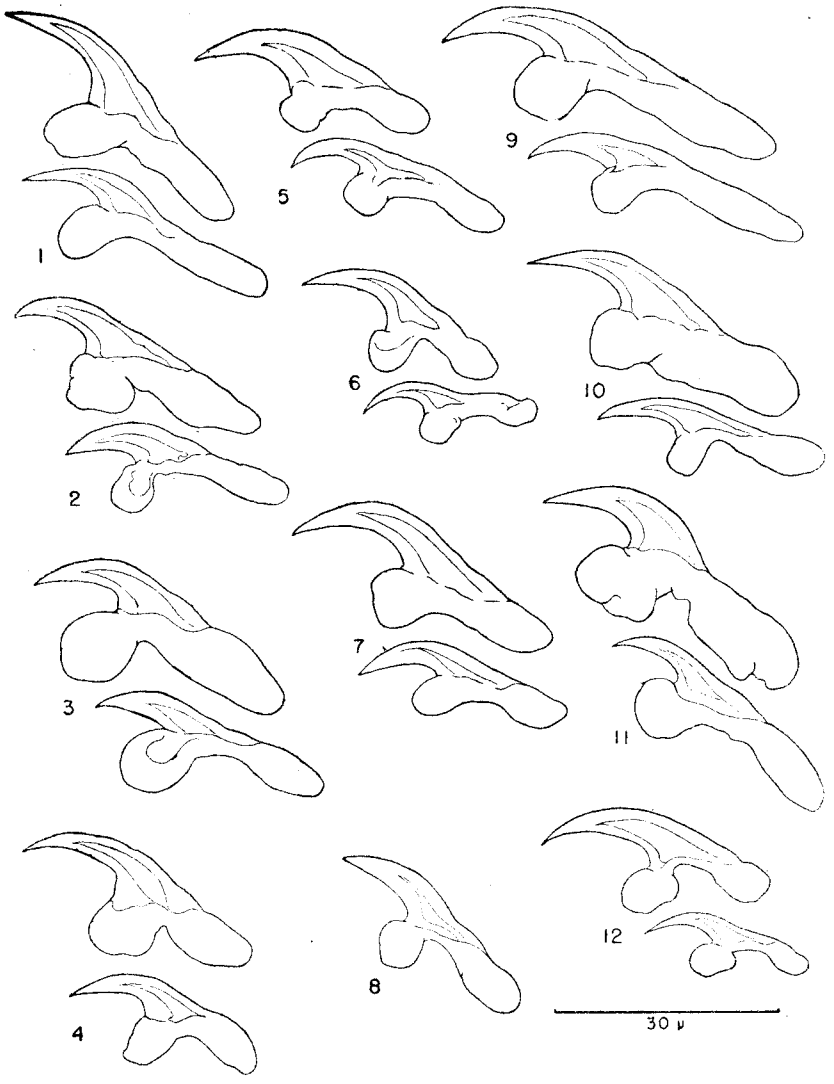

Plate I

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Explanation of Text Figures

Text Fig. 1. Mature segment of *Echinococcus granulosus*, from experimentally infected dog.

Text Fig. 2. Mature segment of *Echinococcus* sp. indet., from experimentally infected arctic fox (*Alopex*).

Explanation of Plate I

Rostellar hook of *Echinococcus* spp. from various hosts and geographic localities. (All drawn to same scale.)

Fig. 1. *E. granulosus*, from domestic dog, Unalakleet, Alaska.

Fig. 2. *E. granulosus*, from jackal (*Canis*), South Africa.

Fig. 3 *E. granulosus*, from domestic dog South Africa.

Fig. 4. *E. granulosus*, from domestic dog, Buenos Aires, Argentina.

Fig. 5. *E. granulosus*, from fox (*Vulpes*), England.

Fig. 6. *E.* ? *granulosus*, from fox (*Vulpes*), Nunivak Island, Alaska.

Fig. 7. *E.* ? *granulosus*, from fox (*Vulpes*), Point Barrow, Alaska.

Fig. 8. *E. granulosus*, from fox (*Vulpes*), Neuchatel, Switzerland. (Large hook only.)

Fig. 9. *E. oligarthrus*, from wild cat (*Felis yaguarondi*), Central America.

Fig. 10. *E. lycaontis*, from wild dog (*Lycaon pictus*), South Africa.

Fig. 11. *E. felidis*, from lion (*Felis leo*), South Africa.

Fig. 12. *Echinococcus* sp. indet., from fox (*Alopex*), St. Lawrence Island, Alaska.